Invited Paper

Butterfly Thermoregulation: Organismic Mechanisms and Population Consequences

Joel G. Kingsolver

Program in Ecology and Evolutionary Biology, Division of Biology and Medicine, Brown University, Providence, Rhode Island 02912

Introduction

Many butterflies regulate their body temperatures in order to meet the thermal requirements for flight. Thermoregulation in butterflies is of interest at two different but complementary levels. First, the physiological and behavioral mechanisms by which Lepidoptera regulate their body temperatures are arguably the most diverse in any group of insects. Second, because of the importance of flight in butterfly biology, thermoregulation provides a vital link relating weather to the population ecology of butterflies.

This review will focus on these two aspects of thermoregulation. Rather than provide a comprehensive summary of thermoregulation in all butterflies studied to date, I shall try to provide a conceptual framework by which to categorize the diversity of thermoregulatory characteristics in butterflies. As a counterpoint to the patterns found in butterflies, I shall also briefly describe the mechanisms of thermoregulation in moths and other insects. I shall use this framework to examine the relation of weather, body temperature, and flight. Finally, I shall summarize recent work in butterfly demography that illustrates the importance of thermoregulation and flight in the population ecology of butterflies.

Mechanisms of Thermoregulation

Most butterflies appear to require elevated body temperatures in order to fly. A survey of 40 species of temperate US butterflies showed that the preferred thoracic temperatures during flight were between 30° and 39°C (Douglas, 1978). (Since the flight muscles are in the thorax, thoracic temperature is the most directly relevant to flight.) More detailed studies of *Papilio* (Rawlins, 1980), *Colias* (Watt, 1968), and *Pieris* (Kingsolver, in press) confirm that thoracic temperatures between 28 and 42°C are required for flight, with rigorous flight restricted to the 33-38°C subrange.

Thus, butterflies appear to be quite similar in their body temperature requirements for flight. These temperatures are similar to those found in many other thermoregulating insects, although slightly lower than those in large moths and in bumblebees (Heinrich, 1981). What are the means by which butterflies achieve and maintain these elevated body temperatures?

Because body temperature is the result of a balance between the rates of heat gain and heat loss, there are two ways of regulating an elevated body temperature: regulation of heat gain, and regulation of heat loss. In addition, there are two different levels at which this regulation of heat gain and loss can occur: regulation of heat production and heat transfer within the body (physiological mechanisms); and regulation of heat exchange between the body and the external environment (behavioral mechanisms). We shall examine both physiological and behavioral mechanisms of thermoregulation, and show how regulation can occur in both heat gain and heat loss.

Physiological Mechanisms

One means of heat gain for thermoregulation is by the metabolic generation of heat, called endothermy. In insects, this heat production results largely from the activity of the thoracic flight muscles, and can occur both during flight and during preflight warmup. During preflight warmup, the muscles that are antagonistic during flight (the wing elevator and wing depressor muscles) are activated simultaneously. These isometrically contracting muscles thus produce heat but little wing movement.

Endothermic heat generation during preflight occurs in a variety of moths, including Saturniids (Kammer, 1968), Sphingids (Heath and Adams, 1967; Kammer, 1970b), and Geometrids and Noctuids (Casey and Joos, 1983), but appears to be quite uncommon in butterflies. The only butterfly reported to date to consistently use endothermic preflight warmup is *Danaus plexippus* (Kammer, 1970a). In *Papilo* preflight endothermy also occurs occasionally, but only in disturbed individuals under conditions too cool for flight (Rawlins, 1980). In both *Papilio* and *Danaus*, endothermy is less effective than behavioral means for increasing body temperature.

During flight, heat is produced by the rapid contraction of flight muscles. Heat production during flight under conditions of low solar radiation has been shown to raise thoracic temperatures by 3-6°C in a number of butterflies, including *Papilio* (Rawlins, 1980), *Danaus* (Kammer, 1970b), and *Colias* (Tsuji *et al.*, in prep.). In contrast, many moths, particularly large Sphingids and Saturniids, achieve thoracic temperatures during flight of 10-20°C above air temperature (Heath and Adams, 1965; Heinrich, 1971; Heinrich and Casey, 1973; Bartholemew and Epling, 1975).

Because the flight muscles are in the thorax, it is thoracic temperature

that is generally regulated most precisely. A variety of studies have documented that insects do not regulate abdominal temperature as precisely as thoracic temperature during flight. The transfer of heat between thorax and abdomen can, however, affect thoracic temperature. One physiological means of regulating this heat transfer is to regulate the circulation of hemolymph.

This mechanism, which has been described for a number of large moths and bees, has been explored in detail in *Manduca sexta* (Heinrich, 1971). During endothermic preflight warmup, thoracic temperature rises rapidly, but abdominal temperature remains near ambient air temperature. During flight at low air temperature, abdominal temperature remains near ambient, but at high air temperatures the abdominal temperature is nearly as high as thoracic temperature. This means that at low air temperature the abdomen loses little heat, but at the high temperature heat loss from the abdomen is substantial (Kammer, 1981).

These patterns result from the hemolymph flow between thorax and abdomen. At high air temperatures the rate of heartbeat is high and the hemolymph flow is rapid. Heat generated in the thorax is rapidly transferred to the abdomen, which is poorly insulated and loses heat rapidly. At low air temperatures the heart and hemolymph flow rates are low, and little heat is transferred and lost through the abdomen. This provides a rather precise mechanism for regulating heat loss and thus thoracic temperature.

While this mechanism occurs in large Sphingid and Saturniid moths, it has not been described in butterflies. The most detailed study to date for thermoregulation during flight in butterflies found no evidence for hemolymph flow regulation (Tsuji *et al*. in prep.). Rawlins (1980) has described abdominal pumping in restrained *Papilio polyexenes* at high air temperatures, which resulted in increased heat loss, but the quantitative importance of this mechanism under natural conditions is unclear.

Another potential means by which hemolymph circulation could affect heat loss is flow in the wing veins. Clench (1966) suggested that hemolymph flow in the wing veins could facilitate heat transfer between the wings and thorax, and contribute to thoracic heating. However, all studies of basking to date refute this hypothesis (Watt, 1968; Wasserthal, 1975; Douglas, 1978). Recent careful measurements of hemolymph flow rates in the wing veins indicate that, at rest, these flow rates are far too slow to significantly affect thoracic temperature (Wasserthal, 1984). The possibility that more rapid flow in the veins during flight could enhance heat loss remains, but this hypothesis will be difficult methodologically to test.

In summary, physiological mechanisms such as preflight endothermy and regulation of hemolymph circulation do not appear to be of general importance in butterflies, while they do occur in many moths and other

insects. Recent mathematical models of heat exchange suggest that, because of the relatively slender body and poor insulation in butterflies, endothermy is simply too expensive energetically (Tsuji *et al.* in prep.). Butterflies rely instead on a variety of behavioral mechanisms for thermoregulation.

Behavioral Mechanisms

The principal way that butterflies regulate heat gain is by behavioral orientation and posture relative to the sun, called basking. Detailed behavioral studies of basking began in the 1950's (Vielmeter, 1954, 1958), and Clench (1966) proposed a classification of basking postures based on wing position. We can describe basking posture in terms of a body orientation angle relative to the sun, and a wing angle (Fig. 1). Using these we can categorize the different basking postures of butterflies (Fig. 2). In dorsal basking, the dorsal surfaces of the thorax and of the wings are positioned perpendicular to the sun ($\gamma = 0°$, $\theta = 90°$). In lateral basking the wings are folded tightly over the dorsum and orient the body and ventral wing surfaces perpendicular to the sun ($\gamma = 90°$, $\theta = 0°$). Body basking posture is similar to dorsal basking except that at least the forewings are only open at a small angle ($\gamma = 0°$, $\theta \geq 5°$).

In body basking, which occurs in Lycaenids and many skippers, the body directly absorbs solar radiation. In the other basking postures, the wings contribute to radiation interception and heat gain. For these postures, wing position and wing color have important thermal effects, which we shall consider in detail.

The physical mechanisms of heat transfer during dorsal basking have been studied in *Papilio*. Wasserthal (1975) showed that the presence of wings could increase the thoracic temperature excess above ambient air temperature by 40-50% in *Papilio*, and that most of these thermal effects are produced by the basal parts of the wings within 5-10 mm of the thorax. These effects appear to be due to two mechanisms. First, radiation is absorbed by the dorsal, basal wing surfaces and the heat is conducted along the wing to the thorax. Because the wing is a relatively poor conductor of heat, only the parts of the wing within a few mm of the thorax can contribute to this process (Kingsolver and Koehl, in press). Second, warm air heated by the wings and body can accumulate beneath the wings, reducing convective heat loss from the thorax (Douglas, 1978). The relative importance of these mechanisms probably depends on wind speed, the latter mechanism dominating at low wind speeds.

Rawlins' (1980) detailed study of dorsal basking in *Papilio polyxenes* also demonstrates the importance of abdomen position relative to the hindwings. During basking, the abdomen is raised above the wings, and is exposed to direct solar radiation. At high ambient temperatures, however, the abdomen is positioned below and shaded by the wings,
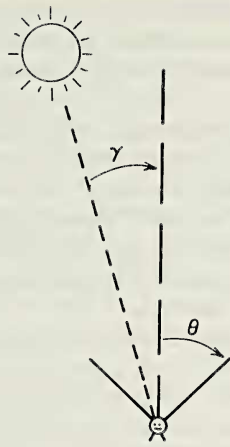
θ : Wing Angle

γ : Orientation Angle

Fig. 1. Diagram illustrating the definitions of body orientation angle (γ) and wing (θ) during basking. From J. G. Kingsolver (1985a), Oecologia, in press.

Basking Postures

$\theta = 0°$
$\gamma = 90°$ or $270°$

$\theta = 90°$
$\gamma = 0°$

$5° < \theta < 90°$
$\gamma = 0°$

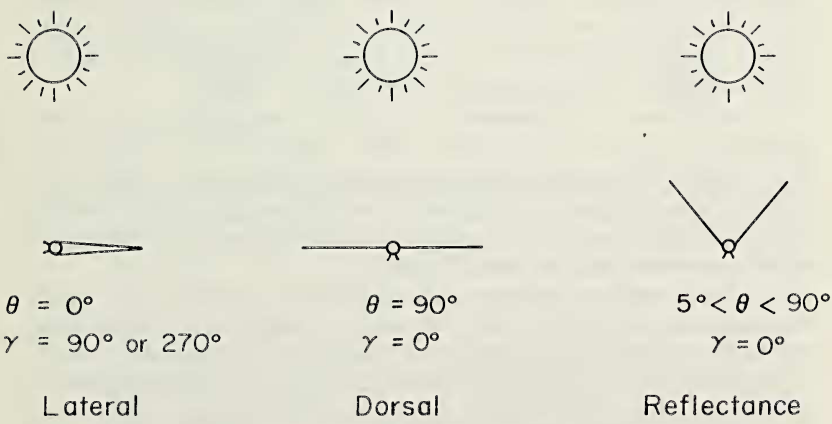Lateral   Dorsal   Reflectance

Fig. 2. Diagram illustrating several common basking postures of butterflies. From J. Kingsolver (1985a), Oecologia, in press.

reducing radiation load and increasing convective heat loss from the wind. In addition, at high temperature the angle of the wings (θ) decreases, and the body orientation becomes nearly random, reducing radiation load.

Dorsal basking is found in many species of Nymphalids, Danaiids, Papilionids, and Heliconiids (Douglas, 1978). A variation of dorsal basking, termed conduction basking, occurs in *Parnassius* and perhaps in other alpine and artic butterflies found in rocky or bare-ground habitats. In conduction basking, the wings are open and the body and ventral wing surfaces are oppressed to the ground, trapping warm surface air and conducting heat from the substrate to the body.

Perhaps the most comprehensive examination of the role of orientation and wing color in butterfly thermoregulation has been in the laterally basking *Colias* by Watt (1968, 1969) and associates (Hoffman, 1974; Tsuji, 1980; Kingsolver, 1983a; Kingsolver and Moffat, 1982; Kingsolver and Watt, 1984). As body temperature increases, *Colias* change their body orientation relative to the sun from perpendicular to random to parallel. During lateral basking the basal parts of the ventral hindwing absorb radiation, and heat is conducted along the wing to the thorax. The proportion of black, melanin scales on the basal, ventral hindwings determines the butterfly's solar absorptivity (defined as the fraction of radiation striking the butterfly which is absorbed by it), and affects thoracic temperature. There is variation among species, and among seasons within species, in the degree of hindwing melanization; in addition in some species temperature and photoperiod conditions during the larval stages can influence adult wing melanization. The result of this variation is that *Colias* occurring in colder habitats have increased melanization; and highly melanized forms can achieve body temperature excesses above air temperature of 15-80% greater than lighter forms. These results are the clearest demonstration of the adaptive significance of wing or body coloration in thermoregulation of insects.

A similar case of photoperiodic effects on melanization for thermoregulation occurs in the lateral basker *Nathalis iole* (Douglas and Grula, 1978). This system of environmental determination of melanization has been implicated in the recent range expansion of this species. Lateral basking is common among Pierids (Coliadinae), and is found in some Lycaenids, Satyrids, and Hesperiids.

There have been no detailed thermal studies of body basking, although it is quite common in Lycaenids, Satyrids, and Hesperiids. It is not clear that radiation absorption by the wings has any thermoregulatory effects in body baskers. It may be that the wing position functions largely to reduce convective heat loss by altering air flow patterns around the body.

A novel basking posture recently described in *Pieris* butterflies

(Kingsolver, in press a, b) is known as reflectance basking (Fig. 2). In this behavior the dorsal thorax is oriented toward the sun ($\gamma = 0°$), and the white wings function as solar reflecting plates that reflect radiation to the body. A detailed examination reveals some non-intuitive relationships between the wing angle used during basking, wing color pattern, and body temperature. For example, if we consider this reflection process from the wings, we can show that the wing angle during basking determines those regions of the wings that can contribute to reflection to the body (Fig. 3). Kingsolver (in press b) developed and tested a mathematical model of reflectance that predicted that butterflies would achieve maximum body temperature at some intermediate basking wing angle, and that the wing angle producing this maximum depends on the extent of melanization at the dorsal margins of the wings. This model correctly predicts that *Pieris* in the subgenus *Pontia*, which have extensive dorsal marginal melanization, achieve maximum body temperatures at and use larger wing angles during basking than those in the subgenus *Artogeia*, which have little
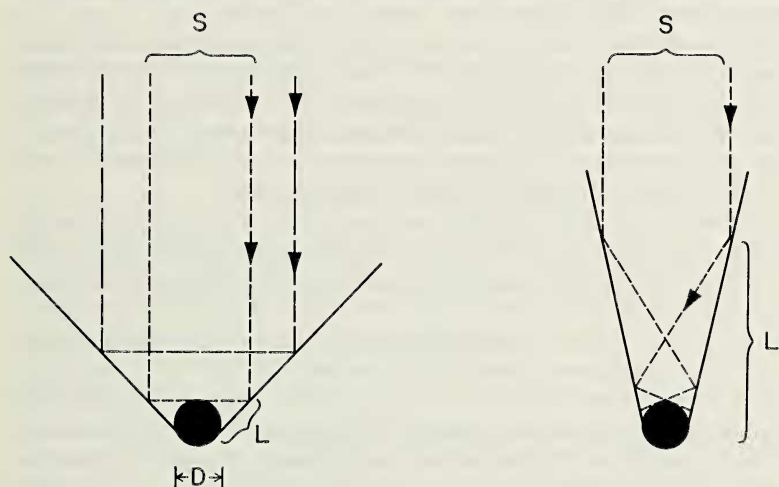

Fig. 3.   Diagram illustrating the reflection of solar radiation from the wings to the body in *Pieris*. The butterfly is considered as a black, cylindrical body with white, flat plates as wings; the figure shows a cross-section through the butterfly perpendicular to the body axis. *D* is the diameter of the body. Beams of radiation (dashed lines) approach the butterfly from above and reflect off the wings. Radiation striking the wings near the body is reflected onto the body, increasing body temperature; radiation striking farther out on the wings is reflected away and does not reach the body. The region of the wings (*L*) that contributes to reflecting radiation to the body is smaller at large wing angles (left panel) than at small wing angles (right panel). From J. G. Kingsolver (1985b), Oecologia, in press.

dorsal marginal variation; the model also correctly predicts behavioral differences in basking between male and female *Pontia*.

These results for reflectance basking are of general interest for two reasons. First, they represent the first demonstration in any insect that the pigmentation pattern on the entire wing surface may be relevant to thermoregulation. Second, reflectance basking requires highly reflective wings: increased melanization in some wing regions can actually decrease body temperature. This effect of melanization is precisely the opposite of that in *Colias, Nathalis,* and other butterflies that use their wings to absorb radiation. Thus, the function of melanization in butterflies depends on the behavioral mechanisms of thermoregulation. Shapiro (see 1976 for a review) and Bowden (1979) have summarized the correlations between climate and melanization, and the environmental determination of melanin deposition, in *Pieris*. These results on reflectance basking suggest that Bowden's (1979) conclusion that most sub-specific variation in the *P. napi* complex is non-adaptive, while perhaps correct, is premature; a more detailed functional analysis will be required.

While, as noted above, several workers have identified particular mechanisms of heat loss that influence body temperature for dorsal baskers (Douglas, 1978; Rawlins, 1980), there have been few systematic studies of the behavioral regulation and determinants of heat loss in butterflies. To date only two systems have been documented in detail: the laterally basking *Colias*, and the dorsally basking *Vanessa cardui*.

Kingsolver and Moffat (1982) examined convective heat loss from real and model *Colias* in a wind tunnel, varying both wind speed and wind direction (yaw angle). Their results indicated that there was no significant effect of wind direction on heat loss, and that the air trapped above the body by the closed wings acted as an insulation layer, reducing heat loss. They also demonstrated that the pubescence on the ventral thorax reduced convective heat loss by 10-70%, and that differences in the thickness of ventral pubescence generated differences in convective heat loss. There are significant differences in the thickness of ventral pubescence among *Colias* species along an elevational gradient in Colorado (Kingsolver, 1983a), with thicker pubescence at higher elevations.

In his wind tunnel study of *Vanessa (Cynthia) cardui*, Polcyn (1984) systematically varied wind direction, wing angle, and the direction of artificial radiation and observed the resulting changes in thoracic temperature excess over air temperature. He showed that wind direction significantly affected body temperature excess, with heat loss being smallest when the tip of the abdomen faced into the wind (i.e., yaw angle = 180°). This effect of wind direction was strongest for dorsal basking and weakest for lateral basking posture. The results suggest that wind direction has larger effects on thoracic temperature than the radiation direction in *Cynthia*, at least for the rather low radiation conditions considered

in the study.

Despite Polcyn's results, there is at present no solid evidence that but-
terflies behaviorally orient to wind direction (except at high wind speeds,
where the response is more likely a mechanical than a thermoregulatory
one) in the lab and the field, even in the careful field studies by Watt
(1968) and Douglas (1978). However, in many instances this lack of
evidence may largely reflect the difficulties of detecting orientation to
wind in the field.

In summary, butterflies largely rely on behavioral means of thermo-
regulation, principally on wing and body orientation to the sun. For at
least certain well studied sytems, we now have a quantitative under-
standing of the mechanisms of heat loss and heat gain that occur for each
major basking posture, except for body basking. Wing color and
melanization at the wing bases can play an important role in thermo-
regulation in lateral and dorsal baskers. Reflectance basking in pierines
provides a unique case in which the entire dorsal wing pigment pattern
can affect body temperature, and in which the thermal effects of
melanization can be opposite of that in other butterflies. This suggests
that we cannot determine the thermal significance of wing pigment pat-
tern without a detailed understanding of the physical and behavioral
mechanisms of thermoregulation. Pubescence on the thorax has been
shown to decrease heat loss, and there are significant differences in the
thickness of pubescence among some congeners that influence body tem-
perature. While there is no evidence that butterflies behaviorally orient to
wind for thermoregulation, recent conflicting results suggest the poten-
tial effectiveness of wind orientation in at least some butterflies.

Weather, Thermoregulation, and Ecology

The Flight Space

Because flight is a temperature-dependent process in butterflies,
weather can influence the occurrence and degree of flight in the field. The
relationship between weather and flight can be summarized by using the
concept of a flight space. The flight space is defined as the ranges of cer-
tain meteorological variables, such as solar radiation, air temperature,
and wind speed, in which flight can or does occur in a particular butterfly
or species of butterfly. Flight spaces have been empirically evaluated in
the field for a number of butterflies, including *Papilio polyxenes*
(Rawlins, 1980), *Colias nastes* (Roland, 1982), *Colias philodice
eurytheme* (Leigh and Smith, 1959), and *Pieris virginiensis* (Cappuccino
and Kareiva, 1985), and reveal considerable differences in flight space
among species. For example, flight in *Papilio polyxenes* is limited to air
temperatures between 19° and 30°C, while in *Colias nastes* flight occurs
between 6 and 20°C. Because these butterflies have similar ranges of body

temperatures for flight, the differences in flight space presumably result from differences in thermoregulatory characteristics and mechanism. Roland (1982) also showed that the degree of hindwing melanization in *C. nastes* is correlated with the lower limit of solar radiation at which flight occurred. In addition, he demonstrated that certain behavioral activities such as courting and oviposition only occurs in restricted regions of the flight space.

Purely empirical investigations of flight space are essential, but at best represent a subset of the entire space. First, the range of weather conditions observed in a particular population or species may cover only a part of the flight space. This limitation can be overcome by transplanting butterflies to sites with different weather conditions (Kingsolver and Watt, 1984). A second, more fundamental limitation is that such empirically-derived flight spaces give little information about the factors determining the size, shape, and position of the flight space. A more general approach is to develop and test models that link thermoregulation to the flight space.

This approach has been used in some detail for *Colias* by Kingsolver (1983a, 1983b; Kingsolver and Watt, 1983, 1984), and is based on the fact that body temperature (T_b) is determined by the balance of the rates of heat inputs (E_{in}) and heat outputs (E_{out}):

$$E_{in} = E_{out} \tag{1 a}$$
$$E_s = E_c + E_t \tag{1 b}$$

where E_s is the rate of solar radiative heat gain, and E_c and E_t are the rates of convective and therman radiative heat loss, respectively. Because E_c and E_t depend on body temperature, equ (1) can be solved to show that body temperature is a function of certain meteorological variables (air and ground temperature, wind velocity, solar radiative load) and certain characteristics of the butterfly (wing color, wing and body area, behavioral orientation, pubescence, and a heat loss coefficient that depends on the size, shape, and position of the butterfly). If we can quantify these butterfly characteristics, we can then predict body temperature under specified meteorological conditions, and use this to identify the set of meteorological conditions in which a given butterfly can achieve the body temperatures needed for flight: i.e., the flight space. Such models have been successfully developed and tested by predicting and then measuring the diurnal patterns of body temperature and flight in several *Colias* populations (Kingsolver, 1983a).

This modeling approach to the study of flight spaces has several advantages. First, one can look at how the differences in thermoregulatory characteristics among species determine the differences in flight spaces. For example, the flight spaces of *Colias philodice eriphyle* and *Colias meadii* differ by about 20%, mainly as a result of the more heavily melanized ventral hindwings of *meadii* (Fig. 4a). Second, one can use the
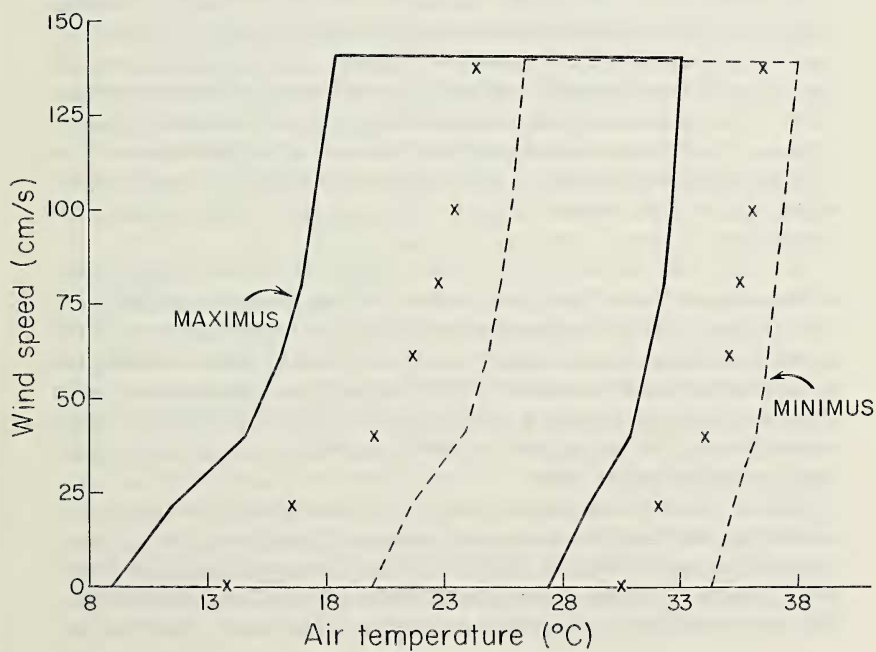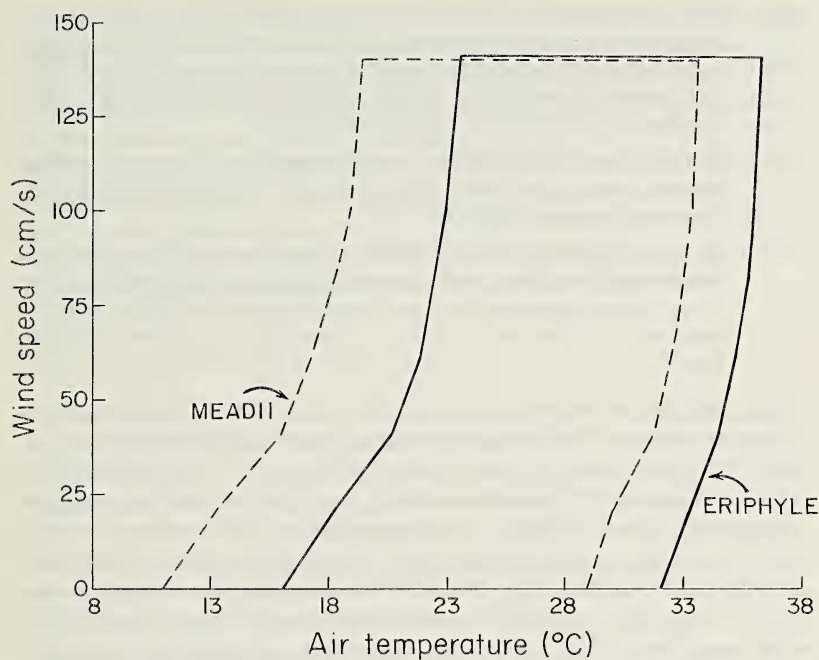
Fig. 4.   Flight space diagrams based on model simulations as a function of wind
          speed (cm/s) and air temperature (°C) for several *Colias* butterflies.
          Solar radiation load perpendicular to the solar beam is 110 mW/CM^2.
          The area enclosed by the lines is the flight space (see text). From
          Kingsolver, J. G. (1983a), Ecology 64:534-545.

          a) *Colias meadii* (dashed line) from Hinsdale Co., Colorado (elevation
          3.6 km) and *C. philodice eriphyle* (solid line) from Montrose Co.,
          Colorado (elevation 1.7 km).

          b) Two hypothetical *Colias* species: *C. maximus* (solid line), with all-
          black wings, back, and a thick pubescence layer; and *C. minimus*, with
          all-yellow wing bases and no thoracic pubescence. The flight space for a
          form with all-black wings and no pubescence (X) is also indicated.
          See text.

flight space to predict the patterns of flight space for a particular species
in various weather conditions. For example, the model predicts that *C. p.
eriphyle* transplanted to the typical habitat of *C. meadii* would not
achieve consistent flight at all—it simply could not achieve the necessary
body temperatures for flight. Actual transplant experiments confirm this
prediction (Kingsolver and Watt, 1984). Finally, one can use the model to
systematically explore the effects of thermoregulatory characteristics
such as wing solar absorptivity on the flight space. For example, wing
color (and absorptivity) in *Colias* is determined by a mixture of two pig-
ment systems: a black, melanin pigment, and a yellow-orange pteridine
pigment mixture. Consider two imaginary, extreme *Colias* 'species': *C.
minimus*, a butterfly with all-yellow wings and no thoracic pubescence,
and *C. maximus*, a butterfly with all-black wings and a thick pubescence
layer. Using the model to generate the flight spaces for these imaginary
'species' (Fig. 4b), one can show that the overlap in flight space is less
than 40%, demonstrating the wide range of meteorological conditions to
which *Colias* can adapt using a rather simple system of thermo-
regulation.

The above discussion of flight space implies that meteorological con-
ditions do not change rapidly relative to the response of the butterfly. In
fact, in many outdoor environments radiation, air temperature, and wind
speed can all change considerably over quite short time periods. Because
of the small size and mass of a butterfly, its body temperature can change
dramatically in 30-60s. As a result, meteorological variation on a time
scale of one to a few minutes are of great importance to insects in general,
and butterflies in particular.

While a number of workers have noted the rapid thermal response of
butterflies, there are few systematic studies of the effects of such varia-
tion for thermoregulation and flight. At the low end of the flight space,
brief periods of cloudiness can drastically reduce flight activity (e.g.
Kingsolver, 1983a). At the high end, brief periods of low wind and/or high

temperature can quickly lead to overheating in butterflies, and it has been shown that such overheating can lead to decreased survivorship and fecundity (Rawlins, 1980; Kingsolver and Watt, 1983). Lederhouse (1982) has shown how such intermittent overheating can force *Papilio polyxenes* males to abandon their defended mating territories. Kingsolver and Watt (1983) have shown that short-term meteorological variation consistently leads to brief periods of overheating and flight cessation in *Colias* butterflies, even at elevations above 3500 m with cool 'average' conditions. These studies suggest that such short-term effects may be of considerable biological importance, and will profit from further investigation.

Thermoregulation and population ecology

Beyond the consequences of overheating for survivorship, fecundity, and territorial defense discussed above, the principal ecological effects of thermoregulation involve the relation of weather to flight activity. These effects can be expressed either in survivorship or fecundity.

The inability to fly because of weather conditions may be an important component of mortality due to predation on adult butterflies. Lederhouse (1983) demonstrated a weather-related increase in mortality in *Papilio polyxenes* that was associated with roosting. Bowers *et al.* (1984) presented evidence based on beak marks for increased bird predation on *Euphydryas chalcedona* that was correlated with unusually cool and cloudy weather. These results suggest that butterflies may be most susceptible to predation during roosting and basking periods when they are unable to attain the body temperatures needed for vigorous flight. However, field experimental tests of this hypothesis have yet to be done.

The relationship of weather, thermoregulation, and realized fecundity has been more closely examfined. In fact, this relationship may play an important role in the population ecology of many temperate butterflies. As a result, we shall consider the determinants of realized fecundity in some detail.

A principal mechanism by which weather and thermoregulation influences fecundity is through limitations on the time available for oviposition activity, which has been examined in some detail for *Colias* in the Colorado Rocky Mountains (Kingsolver, 1983a, b). Along an elevational gradient, there are significant differences among *Colias* populations in the amount of time available for flight activity. Because of the short adult lifespan (4-5 days: Watt *et al.* 1977, 1979; Tabashik, 1980), *Colias* in the higher elevation populations may average only 12-15 h of available flight time during their entire adult lives. Because female *Colias* lay eggs singly on host plants, and need to fly between plants, sufficient flight time is required to locate host plants and lay a full complement of eggs (the maximum fecundity of these species is about 700-1000

eggs: Tabashnik, 1980). In fact, by combining field data on available and realized flight time, activity budgets, longevity, and maximum oviposition rates, Kingsolver (1983b) estimated that *Colias* females in high elevation population can lay only 20-50% of their full complement of eggs as a result of limited flight time.

This suggestion that limited flight time can reduce realized fecundity is supported by several lines of evidence. Flight cage experiments have shown that daily egg production is closely correlated with solar radiation and air temperature in *Pieris rapae* (Gossard and Jones, 1977). Studies with *Colias philodice eurytheme* in environmental chambers showed strong effects of air and body temperature on ovipositon rate (Stern and Smith, 1960). More generally, Courtney (1984) has recently summarized field data on realized fecundity for insects. For Lepidoptera that lay eggs singly, the mean realized fecundity was less than ⅓ of the maximum for all species reported. This strongly suggests the importance of thermoregulation and flight time for fecundity.

An alternative mechanism by which thermoregulation and weather could affect realized fecundity is by influencing the rate of egg maturation (S. Courtney, pers. comm.). Egg maturation rate is a temperature-dependent process in many insects (Wigglesworth, 1972), and thermoregulation by females could increase the maturation rate. While no data are yet available on this possibility in natural conditions, lab and field cage experiments suggest that egg maturation is one component determining oviposition rate (Gossard and Jones, 1977; Stern and Smith, 1960).

The relationship between weather, flight, and fecundity provides us with a useful tool to explore the factors determining the population dynamics of butterflies. In particular one can ask, how does temporal variation in weather affect variation in fecundity and in population size?

One can use the models described above that relate weather to flight time to address this question with the following thought experiment. Consider a female butterfly that emerges on a given day during the flight season, lives and (potentially) lays her eggs during a five-day period, and then dies. What is the expected lifetime flight time available to her? I have used models developed for *Colias* (Kingsolver, 1983a) and solar radiation and air temperature data (mechanical pyranograph and thermograph) from Gothic, Colorado (elevation 2.9 km) to simulate this situation for female *Colias alexandra* in a univoltine population in Gunnison Co., Colorado (Hayes, 1981). The frequency distribution of expected flight time (in hours per five-day lifetime) shows that there is considerable variation within years during a flight season, and between years (Fig. 5). In some years, up to 25% of the population may have 25-30 h of flight time; in other years, 10% of the populations may have less than 5 h. This
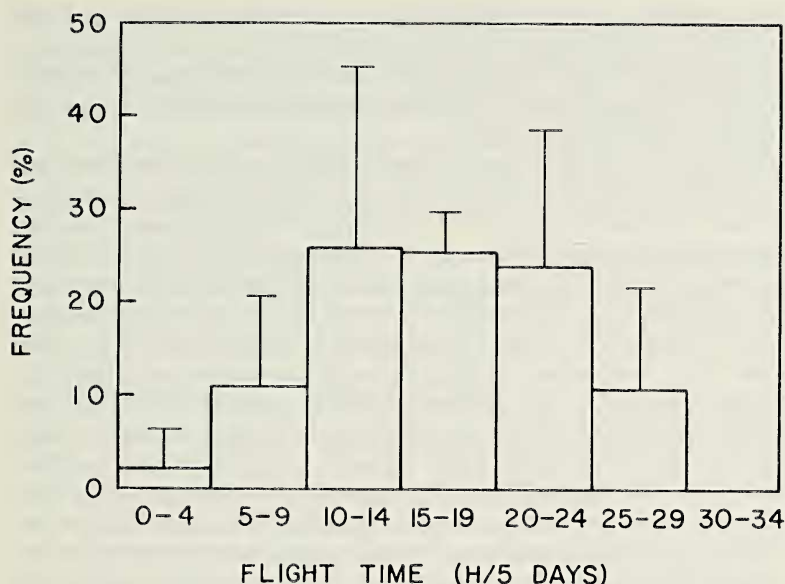
Fig. 5. Frequency distribution of the expected available flight time (in hours per 5-day lifetime) for *Colias alexandra* females in Brush Creek near Crested Butte, Colorado (elevation 2.9 km). The histogram is estimated using the model of Kingsolver (1983a) and solar radiation and air temperature data from Gothic, Colorado, for the month of July (the flight season of *C. alexandra* at this site) for the period 1973-1982. Error bars represent standard deviations of variation among years.

flight time variation would have large effects on variation in realized fecundity both within and between generations. Thus, variation in realized fecundity due to weather variation could affect population fluctuations.

This suggestion that weather and population fluctuations are related *via* flight time and fecundity is supported by a recent review of demographic studies of Lepidoptera by Dempster (1983). He summarized available studies on temperate zone Lepidoptera in which key factor analysis was used to identify that stage or factor in the life cycle that explained the largest amount of the total variation in population size. Of 16 species considered, the single most important factor in 8 species (including *Colias alexandra*; Hayes, 1981) was the failure to lay the full complement of eggs. That is, in 50% of the cases studied, variation in realized fecundity was the single most important determinant of population fluctuations.

It appears, then, that the population dynamics of butterflies may be intimately connected with thermoregulation. I propose that the connec-

tion of weather to population ecology is mediated by thermoregulation and flight in relation to realized fecundity. This proposal both highlights the important role of thermoregulation in butterfly ecology, and provides us with a mechanistic way of studying the effects of weather variation on population dynamics in insects.

In summary, the flight space is a useful tool in summarizing the ranges of weather conditions in which a particular butterfly group can achieve the body temperatures needed for flight. Empirical and modeling approaches have been used to show differences in flight spaces among species, and to identify the morphological and behavioral determinants of these differences. The small body size of butterflies makes them particularly susceptible to short-term weather variation, and it has been shown that overheating resulting from such variation can affect survivorship, fecundity, and territorial defense. Weather conditions that prevent active flight may increase predation on roosting butterflies. More generally, weather limitations on the time available for flight activity may reduce the realized fecundity in many butterflies by limiting the time needed for oviposition. Recent demographic evidence shows that variation in realized fecundity is the single most important factor in fluctuations in population size in many cases. This suggests that weather and thermoregulation may be an important determinant of butterfly population dynamics, through their effects on flight time and oviposition.

Conclusions: Our Current State of Knowledge and Ignorance

1. Physiological mechanisms of thermoregulation are not of general importance for butterflies. Instead, they rely on behavioral mechanisms, in particular on regulation of heat gain by orientation and posture relative to the sun. The behavioral, morphological, and physical determinants of radiation absorption have been studied in some detail; as a result, we now have a quantitative understanding of the principal mechanisms of heat transfer in all of the major basking postures except body basking. On the other hand, the relation of convective heat loss to behavioral orientation to wind has been examined in only two groups, with conflicting results, and its importance for butterfly thermoregulation remains unknown.

2. Surveys of basking posture have been done for many temperate American groups, but we know little of the relative advantages of these postures in different groups, and careful comparative studies within related groups are essential. Basking posture appears to be correlated with both phylogenetic relationship at the family level and body size, but the generality and causal bases for these correlations are unknown. The importance of thermoregulation in tropical butterflies is almost entirely unexplored.

3. Wing color, in particular wing melanization, is an important component of thermoregulation in a number of butterfly groups through its

effects on radiation absorption. In most butterflies, color only at the bases of the wings are relevant to thermoregulation; and color, not pattern, at the wing bases is the key characteristic. One notable exception is for pierine butterflies that use their wings as solar reflecting devices, for which the entire dorsal wing pattern may be relevant to thermoregulation. These studies on the thermal significance of wing color suggest that a detailed understanding of the physical and behavioral mechanisms involved is essential.

4. The flight space is a useful tool in summarizing the ranges of weather conditions in which flight can occur, and has been evaluated empirically and theoretically for a number of butterfly groups. However, the morphological and behavioral characteristics determining the flight space have only been evaluated for one genus.

5. The small body size of butterflies makes them particularly susceptible to weather variation on a time scale of one to a few minutes. In a few well-studied groups, such short-term variation has been shown to affect survivorship, fecundity, flight, and territorial defense.

6. Several lines of evidence suggest that weather-related limitations on the time available for flight activity may reduce realized fecundity by limiting the realized oviposition rate in many temperate butterflies that lay eggs singly. Demographic studies indicate that variation in realized fecundity due to weather variation is a major determinant in population fluctuations in temperate butterflies. Thus, thermoregulation and flight, through their effects on realized fecundity, may be a vital link connecting weather to the population dynamics of many butterflies. A comprehensive experimental demonstration of this system of links, and its general importance for butterflies, is still lacking.

Literature Cited

BARTHOLEMEW, G. & R. EPLING, 1975. Rates of post-flight cooling in sphinx moths. In: *Perspectives of Biophysical Ecology*, D. M. Gates and R. Schmerl (eds.), pp. 405-415, Springer-Verlag, New York.

BOWDEN, S. R., 1979. Subspecific variation in butterflies: adaptation and dissected polymorphism in *Pieris*. J. Lepid. Soc. 33:77-111.

BOWERS, M. D., I. BROWN, & D. WHEYE, 1985. Bird predation as a selective agent in a butterfly population. Evolution, in press.

CAPPUCCINO, N. & P. KAREIVA, 1985. Coping with a capricious environment: a population study of the rare woodland butterfly *Pieris virginiensis*. Ecology 66:152-161.

CASEY, T. M. & B. A. JOOS, 1983. Morphometrics, conductance, thoracic temperature,

and flight energetics of noctuid and geometrid moths. Physiol. Zool. 56: 160-173.

CLENCH, H. K., 1966. Behavioral thermoregulation in butterflies. Ecology 47: 1021-1034.

COURTNEY, S., 1984. The evolution of egg clustering by butterflies and other insects. Am. Nat. 123:176-281.

DEMPSTER, J. P., 1983. The natural control of populations of butterflies and moths. Biol. Rev. 58:461-481.

DOUGLAS, M. M., 1978. The behavioral and biophysical strategies of thermoregulation in temperate butterflies. Dissertation, University of Kansas, Lawrence, Kansas.

DOUGLAS, M. M. & J. GRULA, 1978. Thermoregulatory adaptations allowing ecological range expansion by the pierid butterfly, *Nathalis iole*. Evolution 32:776-783.

GOSSARD, T. & R. JONES, 1977. The effects of age and weather on egg-laying in *Pieris rapae* L. J. Appl. Ecology 14:65-71.

HAYES, J. L., 1981. The population ecology of a natural population of the pierid butterfly *Colias alexandra*. Oecologia 49:188-200.

HEATH, J. & P. ADAMS, 1965. Temperature regulation in the sphinx moth during flight. Nature 205:309-310.

HEATH, J. & P. ADAMS, 1967. Regulation of heat production by large moths. J. Exp. Biol. 47:21-33.

HEINRICH, B., 1971. Temperature regulation of the sphinx moth, *Manduca sexta*. II. Regulation of heat loss by control of blood circulation. J. Exp. Biol. 54: 153-166.

———, 1981. Insect thermoregulation. John Wiley and Sons, New York.

HEINRICH, B. & T. CASEY, 1973. Metabolic rate and endothermy in sphinx moths. J. Comp. Physiol. 82:195-206.

HOFFMAN, R., 1974. Environmental control of seasonal variation in the butterfly *Colias eurytheme*: effects of photoperiod and temperature on pteridine pigmentation. J. Insect Physiol. 20:1913-1924.

KAMMER, A., 1968. Motor patterns during flight and warm-up in Lepidoptera. J. Exp. Biol. 48:89-109.

———, 1970a. Thoracic temperature, shivering, and flight in the Monarch butterfly, *Danaus plexippus*. Z. Vergl. Physiol. 68:334-344.

———, 1970b. A comparative study of motor patterns during preflight in hawkmoths. Z. Vergl. Physiol. 70:45-56.

———, 1981. Physiological mechanisms of thermoregulation. In: *Insect Thermoregulation*, B. Heinrich (ed.), pp. 115-158, John Wiley and Sons, New York.

KINGSOLVER, J. G., 1983a. Thermoregulation and flight in *Colias* butterflies: elevational patterns and mechanistic limitations. Ecology 64:534-545.

———, 1983b. Ecological significance of flight activity in *Colias* butterflies: implications for reproductive strategy and population structure. Ecology 64:546-551.

———, 1985a. Thermal ecology of *Pieris* butterflies: A new mechanism of behavioral thermoregulation. Oecologia, in press.

———, 1985b. Thermoregulatory significance of wing melanization in *Pieris* butterflies: Physics, posture, and pattern. Oecologia, in press

KINGSOLVER, J. G. & M. A. R. KOEHL, in press. Aerodynamics, thermoregulation, and evolution of insect wings: differential scaling and evolutionary change.

KINGSOLVER, J. G. & R. K. MOFFAT, 1982. Thermoregulation and the determinants of heat transfer in *Colias* butterflies. Oecologia 53:27-33.

KINGSOLVER, J. G. & W. B. WATT, 1983. Thermoregulatory strategies in *Colias* butterflies: thermal stress and the limits to adaptation in temporally varying enironments. Amer. Nat. 121:32-55.

————————, 1984. Optimality models and mechanistic constraints: thermoregulatory strategies in *Colias* butterflies. Ecology 65:1835-1839.

LEDERHOUSE, R., 1982. Territorial defense and lek behavior of the black swallowtail butterfly, *Papilio polyxenes*. Behav. Ecol. Sociobiol. 10:109-118.

————————, 1983. Population structure, residency, and weather related mortality in the black swallowtail butterfly, *Papilio polyxenes*. Oecologia 59:307-311.

LEIGH, T. & R. F. SMITH, 1959. Flight activity of *Colias philodice eurytheme* in response to its physical environment. Hilgardia 28:569-624.

POLCYN, D. M., 1984. Effects of wind and light on the equilibrium body temperature of basking butterflies: the role of body orientation and wing position. Masters thesis, University of California, Riverside, CA.

RAWLINS, J. E., 1980. Thermoregulation by the black swallowtail butterfly, *Papilio polyxenes*. Ecology 61:345-357.

ROLAND, J., 1982. Melanism and diel activity of alpine *Colias*. Oecologia 53: 214-221.

SHAPIRO, A. M., 1976. Seasonal polyphenism. Evol. Biol. 9:259-333.

STERN, V. & R. F. SMITH, 1960. Factors affecting egg production and oviposition in populations of *Colias philodice eurytheme*. Hilgardia 29:411-454.

TAQBASHNIK, B. E., 1980. Population structure of pierid butterflies. III. Pest population of *Colias philodice eriphyle*. Oecologia 47:175-183.

TSUJI, J., 1980. The in-flight thermal biology of *Colias* butterflies. Honors Thesis, Stanford University, Stanford, CA.

TSUJI, J., J. G. KINGSOLVER & W. B. WATT. In prep. The thermal biology of *Colias* butterflies during flight.

VIELMETTER, W., 1954. Die Temperaturregulation des Kaisermantels in der Sonnenstrahlung. Naturwissenschaften 41:535-536.

————————, 1958. Physiologie des Verhaltens zur Sonneneinstrahlung bei dem Tagfalter *Argynnis paphia* L. I. Untersuchungen in Freiland. J. Insect Physiol. 2:13-37.

WASSERTHAL, L., 1975. The role of butterfly wings in regulation of body temperature. J. Insect Physiol. 21:1921-1930.

————————, 1984. Hemolymph flows in the wings of pierid butterflies visualized by vital staining. J. Comp. Physiol., in press.

WATT, W. B., 1968. Adaptive significance of pigment polymorphisms in *Colias* butterflies. I Variation in melanin pigment in relation to thermoregulation. Evolution 22:437-458.

————————, 1969. Adaptive significance of pigment polymorphisms in *Colias* butterflies. II. Thermoregulation and photoperiodically controlled melanin variation in *Colias eurytheme*. Proc. Nat. Acad. Sci. 63:767-774.

WATT, W. B., F. S. CHEW, L. G. SNYDER, A. G. WATT & D. E. ROTHSCHILD, 1977. Population structure of pierid butterflies. I. Numbers and movements of some montane *Colias* species. Oecologia 27:1-22.

WATT, W. B., D. HAN & B. E. TABASHNIK, 1979. Population structure of pierid but-
    terflies. II. A 'native' population of *Colias philodice eriphyle* in Colorado.
    Oecologia 44:44-52.
WIGGLESWORTH, V., 1972. The principles of insect physiology. Chapman and
    Hall, London.